

Quaternary Kangaroos (Macropodidae: Marsupialia) from Nombe Rock Shelter, Papua New Guinea, with Comments on the Nature of Megafaunal Extinction in the New Guinea Highlands

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Seven species of macropodids occur in the late Pleistocene-Holocene sediments of Nombe rock shelter, Simbu Province, Papua New Guinea. The four small species, *Dorcopsulus vanheurni*, *Thylogale brunii*, *Dendrolagus goodfellowi* and *Dendrolagus dorianus* are still extant. The three larger species, *Dendrolagus noibano* n. sp., *Protemnodon tumbuna* n. sp. and *Protemnodon nombe* n. sp. are extinct forms known only from Nombe. The two *Protemnodon* species are closest in morphology to Pliocene Australian and New Guinea representatives of the genus and differ markedly from Pleistocene Australian species. The faunal and associated cultural sequence at Nombe provides evidence of long temporal overlap between man and megafauna in montane New Guinea, but at present does not elucidate the causes of large mammal extinction.

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INTRODUCTION

The mountainous island of New Guinea contains a diverse and abundant mammalian fauna. However, the modern fauna is depauperate, especially in large animals, when compared with that present during the Pliocene and Pleistocene. Surprisingly, the Pleistocene fossil record of New Guinea has until now remained almost completely unknown. A single upper molar fragment of a large macropodid from Kafiavana (Plane, 1972) and unallocated diprotodontid, phalangerid and rodent remains from Pureni Swamp (Williams *et al.*, 1972; Hope and Hope, 1976) are the only Pleistocene mammal remains (apart from those from Nombe) thus far recorded. The Pliocene fauna of New Guinea is slightly better known, the rich Awe local fauna having been first noted by Anderson (1937) and described by Plane (1967a, b). The Awe local fauna includes three species of diprotodontids, (*Nototherium watulense*, *Kolopsis rotundus* and *Kolopsoides cultridens*), three macropodids, (*Protemnodon otibandus*, *Protemnodon buloloensis* and a large species of *Dorcopsis*), a dasyurid (*Myoicidis* sp., Archer, 1982), a rodent, cassowary and crocodile. The location of these sites is shown in Fig. 1.

Nombe rock shelter is located in Simbu Province, at 6° 08'S, 145° 10'E, Map reference: Goroka Sheet 7985 (Ed. 1) BP957208, topographic survey, Papua New Guinea: series T601, 1:100,000. The rock shelter is developed in the mid-Eocene to lower Oligocene Chimbu Limestone, and is situated at an altitude of about 1720 metres on the northeast side of the Mt Elimbari ridge. Four main stratigraphic units



Fig. 1. Map showing fossil localities mentioned in the text.

have been discerned in the sediments of the rock shelter (Gillieson and Mountain, 1983, Mountain in press). Most of the specimens described herein were found in the lowest archaeological stratum of the deposits. This stratum (D) consists of a thick, red-brown clay, with little sign of internal stratigraphy. Radiocarbon dating of flowstones occurring in this clay places its accumulation at between 24,000 and 14,000 years B.P., at which time a stream ran through the cave system to feed a spring at the rock shelter. Human artefacts are present throughout this deposit; cultural activity can be documented at the site from 24,000 years B.P. to the present time, although it was not necessarily continuous, especially during the late Pleistocene.

Preliminary analysis of the faunal collection from Nombe by Mountain revealed the presence of a number of extinct marsupials, including a thylacine (*Thylacinus* sp. cf. *T. cynocephalus*), a taxonomically unallocated pig-sized diprotodontid, and several previously unknown species of macropodine kangaroo. These extinct kangaroo species and the four extant kangaroo species found at Nombe are the basis of the present study.

The specimens from Nombe rock shelter described here are to be lodged in the National Museum and Art Gallery of Papua New Guinea and bear the prefix PNG. The Museum catalogue number for the Nombe collection is 82/40; this is followed by an individual number for each specimen described. NCA was the National Antiquities File of Papua New Guinea code for the site at the time of excavation and marking. It has since been altered to PBG but due to lack of space and labour this has not been altered on the specimens. The site prefix is followed by square and level data which define the horizontal and vertical position of the specimen in the site. The name New Guinea is used in a geographic sense and refers to the whole island; Papua New Guinea is the political entity which encompasses the eastern part of the island. Dental terminology and homology follows Archer (1976, 1978). Species and subspecies level taxonomy of extant forms follows Laurie and Hill (1954).

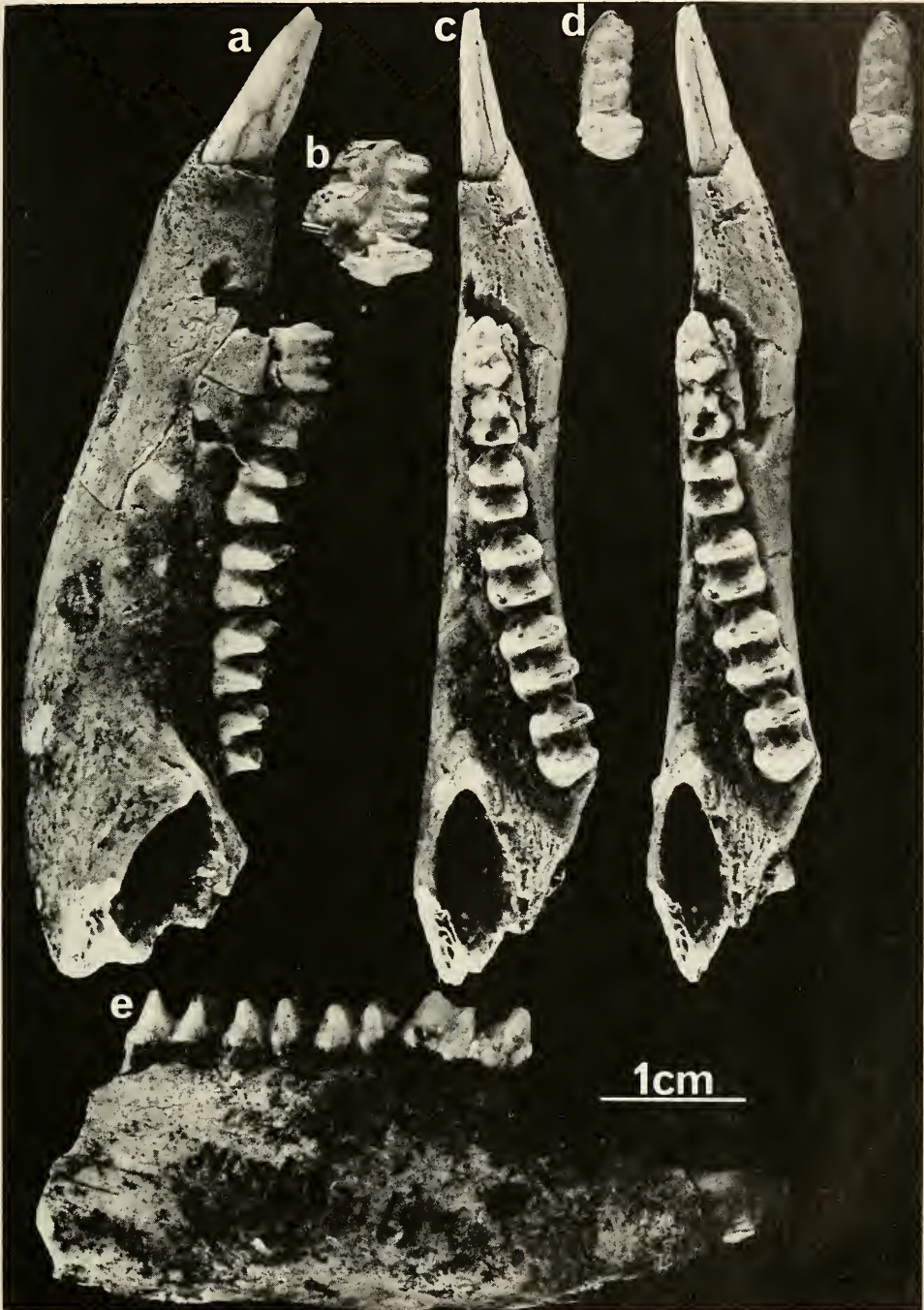


Fig. 2. a, buccal view and b, stereopair of occlusal view of holotype of *Dendrolagus noibano* (PNG/82/40/1), left dentary containing P/2, M/1-5. c, buccal view and d, stereopair of occlusal view of P/3 of holotype of *D. noibano* (removed from crypt). e, buccal view of left dentary of *D. noibano* (PNG/82/40/3) showing great depth of dentary attained with age.

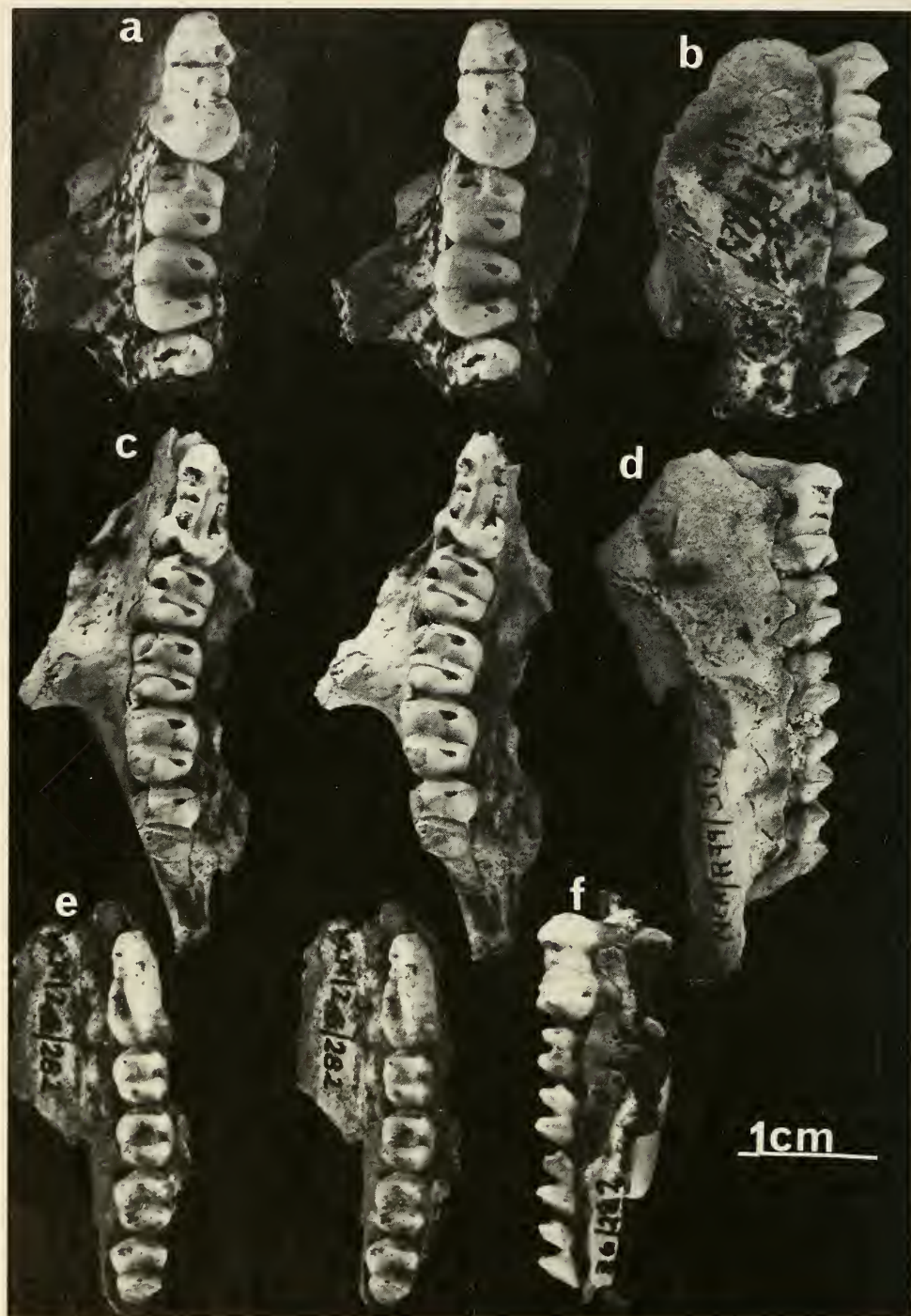


Fig. 3. a, buccal view and b, stereopair of occlusal view of maxilla containing P3/, M2-3/ of *Dendrolagus noibano* (PNG/82/40/4). c, buccal view and d, stereopair of occlusal view of maxilla fragment of *Dendrolagus dorianus* containing P3/, M2-5/ from Nombe rock shelter. e, buccal view and f, stereopair of occlusal view of maxilla fragment of *Dendrolagus goodfellowi* containing P3/, M2-5/ from Nombe rock shelter.

SYSTEMATICS

Superfamily MACROPODOIDEA

Family MACROPODIDAE

Subfamily MACROPODINAE

Dorcopsulus Matschie, 1916*Dorcopsulus vanheurni* Thomas, 1922

The remains of *Dorcopsulus vanheurni* are abundant throughout the archaeological sediments of the Nombe rock shelter including the basal red-brown clay. They do not differ in size or morphology from those of the living species. *Dorcopsulus vanheurni* at present inhabits montane forests of the central ranges of New Guinea (Ziegler, 1977; George, 1973).

Thylogale Gray, 1837*Thylogale brunii* Schreber, 1777

The remains of *Thylogale brunii* are common throughout the archaeological deposits including the red-brown clay. The fossil series is closely similar in size to specimens of the highland race *T. b. keysseri*., and is smaller than the lowland forms *T. b. browni* and *T. b. brunii*. *Thylogale brunii* is widespread in Papua New Guinea, but has not been recorded from montane areas of Irian Jaya except as a subfossil (Hope, 1981). It is found in a variety of habitats, ranging from near sea level to the mountain tops. It makes extensive use of montane grassland, and may be the most abundant large mammal in these areas (Hope and Hope, 1976; George, 1973). The relationships of this endemic New Guinean species of *Thylogale* to the Australian representatives of this genus is at present unknown.

Dendrolagus Muller, 1839*Dendrolagus goodfellowi* Thomas, 1908

Dendrolagus goodfellowi is the smallest of the three species of tree kangaroo found at Nombe. The remains of *D. goodfellowi* are found in all strata, including the red-brown clay, and are indistinguishable in size and morphology from the modern species. Today *D. goodfellowi* inhabits montane forests in eastern New Guinea. *Dendrolagus goodfellowi shawmayeri* (the only subspecies for which any detailed distributional data are available), is reported to occur between 1,200 and 2,750 m on the northern slopes of the central highlands (George, 1978). Groves (1982) has suggested that *D. goodfellowi* is a subspecies of *D. matschiei*. However, until biochemical and morphometric studies are completed these species will be regarded here as distinct, as on the basis of size and morphology at least the typical populations differ considerably.

Dendrolagus dorianus Ramsay, 1883

Dendrolagus dorianus is the largest of the living tree-kangaroos. Males can reach a weight of 18 kg (Ganslosser, 1980). Its remains are found in all layers at Nombe, including the red-brown clay. *Dendrolagus dorianus* is presently found throughout the central cordillera of eastern New Guinea (Groves, 1982). The western highlands form, *D. d. notatus*, is reported to occur only at altitudes above 2,400 m, but further east the typical subspecies is found at lower altitudes (George, 1978). *Dendrolagus dorianus* is thought to be more terrestrial in habit than other species of tree kangaroo (Ganslosser, 1980).

Dendrolagus noibano n. sp.

Figs 2-3, Table 1

Holotype: PNG/82/40/1 (NCA/M71/9), left dentary fragment containing I/1, P/2, P/3 (removed from crypt), M/1-5, but lacking condyle and coronoid process.

TABLE 1

Dental measurements of *Dendrolagus noibano* from Nombe Rock Shelter. L = length, AW = anterior width, PW = posterior width, in mm.

		L	AW	PW
PNG/82/40/4	P3/	11.9	5.6	
	M2/			6.4
	M3/	7.5	6.9	6.6
PNG/82/40/7	P3/	11.8	4.8	7.0
PNG/82/40/5	M4/	7.9	7.5	6.2
PNG/82/40/6	M3/	7.3	6.8	6.2
PNG/82/40/20	P/2	6.2	3.3	3.2
	M/2	7.0	4.8	5.0
	M/3	7.8	5.3	5.5
PNG/82/40/1	P/2	6.5	3.3	4.0
	P/3	12.5	4.4	5.3
	M/1	5.7	3.2	4.0
	M/2	7.4	4.8	5.1
	M/3	8.0	5.5	5.7
	M/4	8.4	6.1	6.2
	M/5	8.5	5.8	5.5
PNG/82/40/3	P/3	10.7	4.0	
	M/2	6.6	4.8	5.0
	M/3	7.6	5.4	5.5
	M/4	8.7	6.1	6.3

Referred specimens: PNG/82/40/2 (NCA/M71/9), left dentary with I/1, P/2, M/2-4 and possibly P/3 (unexcavated) in crypt. PNG/82/40/3 (NCA/M71/9), right dentary with P/3, M/2-4. PNG/82/40/4 (NCA/R79/312), right maxilla fragment containing P3/, M2-4/. PNG/82/40/5 (NCA/792.12/210), left M4/. PNG/82/40/6 (NCA/R79/320), right M3/. PNG/82/40/7 (NCA/792.12/203), right P3/.

Type locality and age: All specimens of *Dendrolagus noibano* are from Nombe rock shelter, Papua New Guinea. Six of the seven specimens were found in the red-brown clay (stratum D) and thus are dated to between 24,000 and 14,000 years B.P. PNG/82/40/7 was found in the mixed levels (stratum C) lying immediately over the top of stratum D and thus probably dates to between 14,000-10,000 BP. There is at present no evidence for the survival of *Dendrolagus noibano* into the Recent period.

Etymology: This species is named after Noibano, the traditional Siame owner of the Nombe rock shelter during the period of excavation by Mountain.

Diagnosis: *Dendrolagus noibano* can be distinguished from all other species of tree-kangaroo by possessing the following characteristics: it is larger than all other forms, and a deep transverse fissure divides the anterior portion of P3/ from the rest of the tooth. It differs from *Dendrolagus lumholtzi*, *D. bennettianus*, *D. goodfellowi*, *D. ursinus* and *D. inustus* in having a large, distinct posterobuccal cuspid developed on P3/. A similar, though less well-developed cuspid is often present in specimens of *D. dorianus* and *D. matschiei*.

Description: Maxilla. The maxilla is represented by a poorly-preserved fragment, with the zygomatic process broken away. The infraorbital canal opens just behind the anterior root of P3/.

P3/. The P3/ is represented by two specimens of which PNG/82/40/7 is the least worn. In both specimens the anterior cusp is strongly ridged, both buccally and lingually. The distinct anterior cusp and anterior-most tubercle of the lingual cingulum are separated from the rest of the tooth by a deep fissure. Between the anterior cusp

and the bulbous posterior cusp are two smaller but prominent cusps with associated buccal ridgelets. A well-developed posterobuccal crest is present on PNG/82/40/7, but is largely broken away on PNG/82/40/4. A discrete posterolingual cusp is present. Two tubercles and a crest which runs anteriorly from the posterolingual cusp make up an irregular lingual cingulum. Only an extremely tiny posterior fossette is present between the main crest and the posterolingual cusp.

Upper molars. The single known M2/ is badly damaged and in an advanced stage of wear. However, the tooth is clearly low-crowned and possesses a very poorly-developed midlink. A slight premetacrista and more clearly-discernible posthypocrista, which runs from the hypocone to the base of the metacone, are present.

The M3/ of PNG/82/40/4 is well-preserved, though worn, with both lophs breached by wear. The tooth is larger than M2/. The anterior cingulum is narrow, running from a point 1 mm linguad of the buccal side of the protoloph and ending approximately 2 mm short of the lingual end of the protoloph. A slight preparacrista connects the paracone to the buccal end of the anterior cingulum. The postparacrista and premetacrista are moderately well-developed and run linguad to converge at a point 2 mm from the buccal end of the median valley. The midlink is very poorly developed. The posthypocrista runs from the hypocone to the base of the metacone on the rear face of the hypoloph.

An isolated upper molar in an early stage of wear, PNG/82/40/5, probably represents the M4/ of *Dendrolagus noibano*. It is low-crowned and larger than M3/. The hypoloph is narrower than the protoloph. The anterior cingulum is relatively narrow, and ends approximately 3 mm short of the lingual end of the tooth. A short vertical preparacrista joins the paracone to the buccal end of the anterior cingulum. No forelink is present. The postparacrista and premetacrista are of similar morphology though better developed than on M3/. The midlink is weakly developed, consisting of a very low postprotocrista which meets a small posterior contribution from the anterior face of the hypoloph. A well-developed posthypocrista joins a weaker, near-vertical postmetacrista on the rear face of the hypoloph.

Dentary. The dentary is relatively shallow in the subadult specimens PNG/82/40/1 and 2, but is greatly deepened in PNG/82/40/3, an older individual. The mandibular symphysis extends to below the P/3 in PNG/82/40/3. The ventral margin of the dentary is nearly straight, but is interrupted by a prominent digastric sulcus and ventral flange. The mental foramen opens just anterior to P/2 or P/3 and the diastema is short. A buccinator groove is present between P/3 and M/3 on PNG/82/40/3. The opening of the masseteric canal is small in the holotype, but this may be due to the immaturity of the animal.

I/1. This tooth is closely comparable in morphology with the I/1 of other species of tree-kangaroo, but is larger. It exhibits dorsal and ventral enamel flanges and a small area of thin ventrolingual enamelling on the crown.

P/2. The P/2 is represented by two relatively unworn, almost identical teeth. They consist of a main blade made up of three evenly spaced, distinct cusps which are subequal in size. Strong buccal and lingual ridges which enclose broad grooves originate from these cusps. The P/2 of *D. noibano* is more similar in morphology to the P/2 of *D. goodfellowi* than it is to that of *D. dorianus*, where the anterior cuspid is usually more distinctly separated from the posterior two. However, extreme variants of P/2 of *D. dorianus* do approach the P/2 of *D. noibano* in morphology.

P/3. The P/3 is known from two specimens, one unerupted and one well-worn. The anterior cuspid is separated from the rest of the tooth by a deep cleft. This cuspid is sharply ridged both anteriorly and posteriorly, the former ending in a distinct, rounded cusple at the anterior-most point of the tooth. The posterior cuspid of the main crest is

offset lingually from the long axis of the tooth. In the holotype a distinct, buccally-directed crest links this cuspid to a larger posterobuccal cuspid. This ridge is absent in PNG/82/04/3, and although the posterobuccal cuspid was clearly present, it is now broken away. Between the posterior and anterior cuspids are two smaller though distinct cuspules. In the holotype these cuspules are isolated from the posterior cuspid by a relatively deep cleft but in PNG/82/40/3 they are united to it to form a continuous blade. The buccal side of the P/3 of the holotype is ornamented by a series of ridgelets and bulges of enamel. These are not as evident on the referred specimen, where they may have been reduced by wear.

Lower molars. The hypolophid of the only known M/1 (the holotype), is breached by wear, and a small portion of the lingual side of the protolophid is missing. The trigonid of M/1 consists of a well-developed longitudinally oriented paracristid and a barely-developed lophid, the latter oriented with its long axis rotated at approximately 30 degrees clockwise relative to the hypolophid. The hypolophid is well-formed. The cristid obliqua is barely visible, running between the hypoconid and the posterior surface of the protoconid. The preentocristid is strongly-developed. In general, the trigonid morphology of *D. noibano* is most similar to that of *D. goodfellowi*, and differs from that of *D. dorianus*, which displays a better-formed, more nearly transverse protolophid.

The M/2 of the holotype is virtually unworn. It is a low-crowned and rather bulbous tooth, with the protolophid slightly narrower than the hypolophid. The anterior cingulum is narrow and anteroposteriorly short. The paracristid and cristid obliqua are very poorly-developed, the latter running just linguad of the protoconid. Distinct though small premeta- and preentocristae are present, running perpendicular to the molar lophids. The rear face of the hypolophid is swollen but no posterior cingulum is present.

The M/3 differs from M/4 in being larger and having the protolophid and hypolophid subequal in width. The paracristid and cristid obliqua are better-developed.

The M/4 is larger than the M/3 and has a slightly better-developed cristid obliqua and paracristid. The anterior cingulum is broader.

The M/5 differs from M/4 in being narrower, in having a more poorly-developed preentocristid and an anterior cingulum that is slightly less extensive buccally.

Discussion: On the basis of dental morphology, *Dendrolagus noibano* appears to be most closely related to *D. dorianus* and *D. goodfellowi*. Along with *D. matschiei* and *D. ursinus*, these four extant species form a derived group of tree kangaroos which are definable on the basis of hindlimb morphology (Flannery and Szalay, 1982). *D. noibano* clearly belongs within this group, which is endemic to New Guinea, and not within the more plesiomorphic grouping of Flannery and Szalay, which contains the remaining New Guinean and both Australian species of *Dendrolagus*.

Similarities between *D. noibano* and *D. goodfellowi* include features such as the compressed trigonid on M/1 and the evenly-spaced cuspids on P/2. These are probably primitive retained characteristics, as they are seen in primitive tree-kangaroos and/or other macropodines, and thus do not indicate a close phylogenetic relationship. However, features shared with *D. dorianus*, such as the presence of large buccal cuspids on P3/ and P/3 are derived states, and appear to indicate a close relationship between these forms.

On the basis of P3/3, M3/ and M/4 measurements, *D. noibano* is 13% larger on average than *D. dorianus* (see Table 2). While *D. noibano* and *D. dorianus* are closely related it is thought unlikely that they represent components of a dwarfing lineage, in the sense of Marshall and Corruccini (1978), for several reasons. First, the remains of

TABLE 2

Measurements of P3/, P/3, M3/ and M/4 for a modern sample of *Dendrolagus dorianus* held in the Australian Museum, and *Dendrolagus noibano*. Based on mean measurements, the *D. noibano* material is 13% larger in average than that of *D. dorianus*. L = length, AW = anterior width, PW = posterior width, \bar{x} = mean, R = range, N = sample size, STD = standard deviation.

			<i>D. dorianus</i>	<i>D. noibano</i>
P3/	L	\bar{x}	10.8	11.9
		R	10.3-11.5	11.8-11.9
		N	12	2
		STD	.40	
	AW	\bar{x}	5.1	5.2
		R	4.5-5.7	4.8-5.6
		N	12	2
		STD	.41	
	PW	\bar{x}	6.5	7.0
		R	6.0-7.1	
		N	12	1
		STD	.31	
P/3	L	\bar{x}	9.7	11.6
		R	8.8-10.4	10.7-12.5
		N	12	2
		STD	.47	
	AW	\bar{x}	3.8	4.2
		R	3.4-4.7	4.0-4.4
		N	12	2
		STD	.41	
	PW	\bar{x}	4.2	5.3
		R	3.6-5.0	5.3
		N	12	
		STD	.4	1
M3/	L	\bar{x}	6.7	7.4
		R	6.2-7.3	7.3-7.5
		N	12	2
		STD	.3	3
	AW	\bar{x}	6.7	6.9
		R	6.2-7.3	6.8-6.9
		N	12	2
		STD	.34	
	PW	\bar{x}	6.1	6.4
		R	5.7-6.5	6.2-6.6
		N	12	2
		STD	.26	
M/4	L	\bar{x}	6.8	8.6
		R	6.3-7.2	8.4-8.7
		N	12	2
		STD	.29	
	AW	\bar{x}	5.5	5.8
		R	5.0-5.8	5.4-6.1
		N	12	2
		STD	.23	
	PW	\bar{x}	5.4	6.3
		R	5.0-5.6	6.2-6.3
		N	12	2
		STD	.2	3

both species are present in strata D and C at Nombe, and thus the species were contemporaneous if they were not actually sympatric and, second, considerable morphological differences in P3/, P2, P/3, and M/1 exist between these species.

Dendrolagus noibano is a relatively rare element in the fauna of the Nombe rock shelter compared with the other tree-kangaroos, being represented by a minimum number of 3 individuals. It is also the smallest extinct macropodid at Nombe. Given the sharp cut-off of living and extinct species at this point, the relatively small size difference between *D. noibano* and *D. dorianus* may have been a crucial one in terms of survival or extinction in late Pleistocene New Guinea. Unfortunately, post-cranial remains referable to *D. noibano* have yet to be isolated in the collections, and thus its degree of arboreal adaptation cannot be established. Large size alone may not have barred it from an arboreal existence, as Flannery and Szalay (1982) have described a gigantic and apparently at least partly arboreal tree kangaroo from New South Wales.

Protemnodon Owen, 1874

Protemnodon tumbuna n. sp.

Figs 4-5, Table 3

Holotype: PNG/83/40/8 (NCA/792.11/177), right maxillary fragment containing P2/M1-2/, P3/ removed from crypt. The premaxillary and nasal sutures are partly preserved.

Referred specimens: PNG/82/40/18 (NCA/Z6/324), left I1/. PNG/82/40/9 (NCA/H71/9), right dentary fragment containing P2, P/3 (in crypt), M/1-3, M/4 (in crypt). PNG/82/40/10 (NCA/Z6/311, R79/312, R79/313), left dentary containing I/1, P/3, M/2-5. PNG/82/40/11 (NCA/D79/90), left dentary fragment with roots of P/3, M/2. PNG/82/40/12 (NCA/TT/39), right M4/. PNG/82/40/13 (NCA/A5/336), left M/1. PNG/82/40/14 (NCA/A4/3), right I/1. PNG/82/40/15 (NCA/H71/9), right I/1. PNG/82/40/16 (NCA/D79/338), right I/1. PNG/82/40/17 (NCA/D79/73), left I/1.

Type locality and age: All specimens are from Nombe rock shelter, Papua New Guinea. Nine specimens were found in the red-brown clay (stratum D), which was deposited during the late Pleistocene, between 24,000 and 14,000 years BP. The holotype was found in the mixed levels (stratum C) that overlie the clay and which are dated at between 14,000 and 10,000 BP. Specimen PNG/82/40/11 was found in the bone level (stratum B) which overlies the mixed levels. The bone level dates to a period after 10,000 years BP. Unlike most of the pieces found in the lower levels, the specimen is burnt. There are very few specimens of extinct macropodids present in the stratum B levels, and there is some reason to believe that those found there have been redeposited from the red-brown clay. At the back of the shelter is a trench, dug during the accumulation of stratum B which extends into the clay of stratum D (the layer containing most of the specimens discussed in this paper). A few specimens may have been dug up from their original context and become part of the refuse at stratum B, becoming thoroughly burnt in the process. It may be possible to test this hypothesis by chemical analysis in the future.

Etymology: The species name *tumbuna* means ancestor or of the ancestors in Neo Melanesian Pidgin. It is used in double allusion, first in reference to the primitive morphology of some aspects of the dentition the species, and, second, to its association with the Pleistocene human inhabitants of highland Papua New Guinea.

Diagnosis: *Protemnodon tumbuna* can be distinguished from other species of *Protemnodon* by possessing the following characteristics. The main crest of the P3/ is strongly concave buccally and bears a sharp, raised lingual cingulum which lacks tubercles. This type of morphology is otherwise only approached in some variants of *P. otibandus*, e.g. CPC69857. In other species of *Protemnodon*, the main crest is shorter and the lingual



Fig. 4. a, buccal view and d, stereopair of occlusal view of holotype (PNG/82/40/8) of *Proteomnodon tumbuna* containing P2/, M1-2/. b, stereopair of occlusal view and c, buccal view of P3/ of holotype of *P. tumbuna* (removed from crypt). e, stereopair of occlusal view and h, buccal view of M4/ (PNG/82/40/12) of *P. tumbuna*. f, stereopair of occlusal view and i, buccal view of M1/ (PNG/82/40/13) of *P. tumbuna*. g, lingual view of PNG/82/40/14, right I/1 of *P. tumbuna*. j, buccal view of left dentary (PNG/82/40/10) of *P. tumbuna*, containing P/3, M/2-5.



Fig. 5. a, stereopair of occlusal view of left dentary (PNG/82/40/10) of *P. tumbuna*, containing P/3, M/2-5. b, stereopair of occlusal view and c, buccal view of PNG/82/40/9, right dentary fragment of *P. tumbuna* containing P/2, M/1-4 (M/4 in crypt). d, stereopair of occlusal view and e, lingual view of P/3 (removed from crypt of PNG/82/40/9).

TABLE 3

Dental measurements of the species of *Protemnodon* from Nombe rock shelter. L = length, AW = anterior width, PW = posterior width, JD = diastema length, in mm.

		L	AW	PW
<i>Protemnodon tumbuna</i>				
PNG/82/40/8	P2/	10.0	6.0	7.3
	P3/	15.1	8.0	8.9
	M1/	8.7	7.2	8.0
	M2/	10.4	9.6	9.8
PNG/82/40/12	M4/	11.9	10.4	10.0
PNG/82/40/9	P/2	8.9	4.5	4.8
	P/3	14.4	3.7	5.6
	M/1	8.2	5.8	6.3
	M/2	9.8	7.4	
	M/3	12.1	8.7	9.0
PNG/82/40/13	M/1	9.5	6.5	7.0
PNG/82/40/10	P/3			5.3
	M/2	9.9		8.0
	M/3	11.8	8.6	8.7
	M/4	12.4	9.4	9.8
	M/5	13.2	9.4	8.6
<i>Protemnodon nombe</i>				
PNG/82/40/23	JD	21.0		
	P/3	12.2	4.5	5.3
	M/2	8.0		6.6
	M/3	9.8	7.6	8.0
	M/4	11.2	8.8	8.8
	M/5	11.4	8.9	8.3
PNG/82/40/19	JD	24.0		
	P/3	11.7	4.0	5.0
	M/2	7.7		
	M/3	9.5	7.0	7.1
	M/4	10.8	8.0	7.9
	M/5	11.5	8.2	7.2

cingulum is blunter and composed to some extent of low tubercles. On P2/ of *P. tumbuna*, the lingual cingulum extends far anteriad and is united to the main crest by an accessory cingular crest. In other species the lingual cingulum joins the main crest more posteriorly and there is no accessory cresting. The anterior upper molars of *P. tumbuna* have a weak postlink present on the rear face of the hypoloph, a feature otherwise seen only in *P. otibandus*. The preparacrista is virtually absent on upper molars of *P. tumbuna*, being better developed in other forms. In common with *P. roechus* and to a lesser extent *P. otibandus*, the I/1 lacks a sharp ventral enamel flange in its posterior portion. The coronoid process of the dentary ascends at a steeper angle than in other *Protemnodon* species where this structure is preserved.

Description: Maxilla. The maxillary fragment of the holotype preserves a portion of both the nasal and premaxillary suture. The premaxillary suture is nearly vertically oriented with respect to the tooth row, and the nasal suture is straight and horizontally oriented. The infraorbital canal opens above the midpoint of P2/. A shallow fossa is present between the anterior rim of the orbit and the infraorbital foramen.

I1/. The single, left I1/ known is heavily worn. The root is laterally compressed and oval in cross section. The wear facet slopes gently dorsally and posteriorly from the anterior margin. Enamel is restricted to the anterior face of the tooth.

P2/. The P2/ is short but broad, being subequal in length to the M2/. The main crest is composed of distinct anterior and posterior cusps and a single medial cuspule with associated buccal and lingual ridgelets. The buccal surface of the tooth is further ornamented by strong cresting from the principal cusps. A broad posterolingual blade joins the main crest to form the posterior portion of a continuous high lingual cingulum. The lingual cingulum joins the main crest anteriorly by two cristae, one joins the main crest in the centre of the anterior cusp, and is clearly the analogue of the structure that joins the lingual cingulum to the main crest in other *Protemnodon* species, while another weaker crest connects the lingual cingulum to the main crest at the anteriormost point of the tooth. This crest is unique to *P. tumbuna* amongst near relatives and is probably a neomorphic structure.

P3/. The P3/ is relatively short and slightly broader posteriorly than anteriorly. The main crest is strongly concave buccally. Distinct anterior and posterior cuspids are present, the former with strong buccal and anterior and weaker lingual cresting. Between these cusps the main crest is somewhat irregular and crenulate. Two weak ridgelets are present on the buccal and lingual faces, the buccal pair enclosing a small fossette. The obliquely oriented posterolingual blade is slightly lower than the main crest. Two ridges run between these structures to enclose a small posterior fossette.

Upper molars. The M1/ of the holotype is slightly worn, both lophs being breached by wear. It is extremely low-crowned. The lingual margin of the tooth is more gently inclined towards the tooth base than is normally seen in macropodoids, resulting in a marked constriction of the loph apices. The protoloph is slightly narrower than the hypoloph. A weak preparacrista joins the protoloph to the buccal end of the lingually restricted anterior cingulum. A very weak forelink is present. The midlink is worn but was evidently poorly-developed. A well-developed postparacrista and premetacrista converge in the median valley, approximately 3 mm lingual of the buccal margin of the tooth. The postmetacrista is extremely weakly-developed, running almost vertically down the rear face of the hypoloph. The posthypocrista is well-developed; it swings buccally to disappear midway across the rear of the molar.

The M2/ is similar to the M1/ in being low-crowned and in displaying a gently-inclined lingual side. However, it is larger, and differs from that tooth in the following ways. The preparacrista is barely indicated and does not contact the anterior cingulum. The anterior cingulum is slightly more extensive though no forelink is present. The midlink and all accessory cresting are better-developed, with the exception of the premetacrista, which is distinctly weaker than the postparacrista. A low crest descends the anterior face of the hypoloph to join the midlink. A distinct but small postlink is present near the apex of the hypoloph midway along its length.

The M4/, PNG/82/40/12, differs from the M2/ in being larger, having a more steeply-inclined lingual margin and in being subequal in anterior and posterior width. The tooth is also slightly higher-crowned (which may be due in part to its being unworn). The anterior cingulum extends further lingually than on M2/. The postparacrista appears to be stronger although this may also be a reflection of wear. The premetacrista is weaker. The postlink is reduced to a slight fold of enamel on the rear face of the hypoloph. The posthypocrista and postmetacrista are more strongly developed, the latter forming a broad shelf at the base of the posterior fossette.

Dentary. In the adult specimens the mandibular symphysis is extensive and rugose, and extends to below the anterior end of P/3 on the holotype. The ventral border of the dentary is almost straight and bears a poorly-developed digastric sulcus and ventral ridge. The opening of the masseteric canal is moderately large. The anterior border of the coronoid process rises sharply, leaning forward at an angle of less than 90 degrees to the molar row. The large mental foramen lies just below and anterior to P/3. The

diastema is short. A poorly-defined buccinator groove extends below the cheektooth row from P/3 to the midpoint of M/4.

I/1. Five specimens of I/1 are known, one of which (PNG/82/40/10) is retained within a dentary. These teeth are relatively narrow and lanceolate in form, being similar to those of *Protemnodon otibandus*, and do not display the spatulate morphology seen in *P. roechus*. On unworn examples, it can be seen that the tooth is thickly enamelled buccally and ventrolingually. The crown possesses a dorsal and ventral enamel flange. On the posteroventral portion of the tooth, enamel continues posterior to the flange as a rounded hump.

P/2. The single known P/2 (PNG/82/40/9) is only slightly worn. The tooth is short and bulbous relative to that of *Protemnodon otibandus*. The anterior cuspid forms the highest point on the crest, and is slightly buccally offset from the main crest. This cuspid bears a strong buccal crest which terminates before reaching the crown base. Shallow grooving on the buccal and lingual faces of the tooth suggest that two faint cuspules may have been present between the anterior and posterior cuspids. The posterior cuspid is blade-like, and is flexed lingually out of alignment with the main crest. A distinct but narrow groove demarcates the posterior cuspid on its lingual side.

P/3. The unerupted P/3 of PNG/82/40/9 is almost complete and is unworn. It is a relatively elongate tooth consisting of a straight longitudinal crest and prominent anterior and posterior cuspids. The anterior cuspid is slightly offset buccally from the main crest, and bears three ridges, one on each of its buccal, lingual and anterior sides. Between the main cusps are two distinct cuspules with associated buccal and lingual ridgelets. These are subequal in height to the anterior cuspid, but lie somewhat below the high posterior cuspid. A low cingulum in the form of a basal enamel bulge is present on the buccal side of the tooth. The base of the crown on the lingual side is broken away. The P/3 fragment of PNG/82/40/10 differs from that described above in that the two cuspules are more sharply defined and larger, the tooth overall is more bulbous, and the base of the lingual side of the crown is preserved, showing that the basal cingulum is barely distinguishable on that side.

Lower molars. The M/1, known from two specimens, is low-crowned and is quite bulbous basally, particularly on the buccal margins of the lophids. The protolophid is slightly narrower than the hypolophid. The anterior cingulum is very short and low but extends to the lingual side of the tooth. The paracristid runs from the apex of the protoconid to intersect the anterior cingulum at a point just buccal of the midline of the tooth. The premetacristid is well-developed and runs from the apex of the metaconid to the lingual end of the anterior cingulum. A poorly-defined fossette is present between the paracristid and the buccal extension of the anterior cingulum. The cristid obliqua is rather poorly-developed and runs to a point well buccal to the midline of the tooth. A well-developed preentocristid and a posterior cingulum are present, the latter being confined to the buccal half of the tooth.

The M/2 of PNG/82/40/9 is only lightly worn, but the entoconid is broken away. It is similar to the M/1 in overall form but differs in the following details. The protolophid and hypolophid are more nearly subequal in width. The paracristid and cristid obliqua are better-defined, the latter crest originating well below the apex of the hypoconid. Both crests swing further linguad, and the anterobuccal fossette is correspondingly better-defined. The protolophid contribution to the cristid obliqua is also better-defined. The premetacristid is less extensive anteriorly, just failing to contact the anterior cingulum; a faint accessory cristid curves buccally for a short distance below the metaconid apex. A weak postmetacristid runs buccally to a point just linguad of the cristid obliqua. The posterior cingulum is well-developed, but is restricted to the buccal two thirds of the tooth.

The M/3 of PNG/82/40/9 is unworn and complete. It differs from M/2 in the following ways. The anterior cingulum is short and less extensive lingually. The protoconid is rotated anteriorly relative to the metaconid. The paracristid is strongly sinuous in form, swinging lingually and then anteriorly to contact the anterior cingulum just buccal to the midline of the tooth. The cristid obliqua is slightly better-developed, originating about 3 mm below the apex of the hypoconid and ending midway across the rear face of the protolophid. The hypoconid is noticeably taller than the entoconid, and is positioned lingually relative to the protoconid. A distinct although weakly-developed preentocristid is present, originating from the apex of the entoconid it runs anteriorly, then turns sharply buccally to terminate just lingual of the anterior end of the cristid obliqua; the anterobuccal portion of a similar crest is just preserved in M/3 of PNG/82/40/10. The posterior cingulum of PNG/82/40/9 is well developed but restricted to the buccal two thirds of the tooth. In the M/3 of PNG/82/40/10 it is both broader and more extensive lingually.

The M/4 and M/5 are known only from PNG/82/40/10. The M/4 differs from M/3 in the following ways. It is larger. The paracristid forms a straight crest between the protoconid and the anterior cingulum at the midline of the tooth. The anterior cingulum is lower and less extensive lingually. The cristid obliqua runs to a point on the midline of the tooth as in M/3. The buccally-directed preentocristid may be slightly better developed. The posterior cingulum is similar to that of M/3 of the same specimen (PNG/82/40/10). The degree of protoconid and hypoconid rotation cannot be established as the specimen is worn.

The M/5 differs from M/4 in the following ways. The anterior cingulum is anteroposteriorly lengthened but is less extensive lingually. The cristid obliqua is less well-developed, forming a low, rounded enamel hump. The hypolophid is narrower than the protolophid. The premetacristid and preentocristid are marginally better-developed, the latter running more nearly vertically down the lingual margin of the hypolophid. The posterior cingulum is less extensive buccally but more extensive and broader lingually.

Discussion: *Protemnodon tumbuna* most closely resembles Pliocene New Guinean and (more distantly) Pliocene Australian species of *Protemnodon*. The similarity between these forms is due primarily to a retention of many plesiomorphic states such as low-crowned molars, the presence of a weak postlink on upper molars and the lanceolate form of I/1. However, the high continuous lingual cingulum of P3/ in *P. tumbuna* and some specimens of the Pliocene New Guinean *P. otibandus* may be a derived characteristic linking these forms, as may be the unusual ventral enamel distribution of I/1. Many features of *P. tumbuna* are, however, unique or apomorphic within *Protemnodon*. Included here are the short, buccally-concave main crest of P3/, the anterior linking of the lingual cingulum and the bulbous nature of P2/, the short, bulbous P/2 and the steep angle of ascent of the coronoid process of the dentary. Thus if, as appears likely, *P. tumbuna* is descended from a *P. otibandus*-like ancestor, the lineage has undergone substantial morphological change during the late Pliocene-Pleistocene.

Protemnodon tumbuna, represented by a minimum number of four individuals, is the largest macropodid and the second largest marsupial (the largest being a diprotodontid) in the fauna of the Nombe rock shelter. *P. tumbuna*, however, is small compared with extinct Australian Pleistocene macropodids, and was probably smaller than several living Australian macropodids (the species of *Macropus* and some *Osphranter*). It seems most likely that *P. tumbuna* inhabited rainforest areas, as its molars are very low-crowned, as are those of living rainforest-inhabiting macropodids (e.g. the species of *Dorcopsis*, *Dorcopsulus* and *Dendrolagus*). *Thylogale brunii*, which may be locally

very abundant in montane grassland habitats in New Guinea has considerably higher-crowned molars than any of these forms including *P. tumbuna*.

Protemnodon nombe n. sp.

Figs 6-7, Table 3

Holotype: PNG/82/40/23 (NCA/M71/9), right dentary containing root of I/1, P/3, M/2-5 but lacking most of the dentary posterior to M/5.

Referred specimen: PNG/82/40/19 (NCA/R79/313, NCA/R79/314, NCA/R79/297, NCA/R79/312), left dentary containing broken I/1, P/3, M/2-5 but lacking much of ascending ramus.

Locality and age: Both specimens of *Protemnodon nombe* were recovered from the red-brown clay (stratum D) of Nombe rock shelter, which is dated to between 24,000 and 14,000 years BP.

Etymology: The species is named for the type and only known locality of *Protemnodon nombe*, the Nombe rock shelter.

Diagnosis: *Protemnodon nombe* is the smallest species of *Protemnodon* known. It is closest in size to *P. buloloensis* of the Pliocene Awe local fauna of New Guinea, but differs from that form in having a proportionately much shorter P/3, less elongate molars and a longer dentary diastema. Its molars are lower crowned than those of *P. anak*, *P. devisi* and *P. newini*. It differs from *P. tumbuna* by possessing a narrow I/1 which has a distinct ventral enamel flange which extends to the posterior end of the crown, by a much less strongly-ridged P/3, a relatively narrower anterior cingulum on lower molars, a proportionately broader angle of the dentary, and a more swollen masseteric canal.

Description: Dentary. Much of the description of the dentary is based on the referred specimen (PNG/82/40/19), as it is more complete. The dentary is relatively narrow and slender below the cheektooth row, but is nonetheless quite large relative to tooth size. The diastema is relatively short, but less so than in *P. buloloensis*. The mental foramen is positioned well forward of the anterior root of P/3. The mandibular symphysis appears to have been less extensive than in *P. tumbuna*. The ventral margin of the horizontal ramus is gently concave below the posterior molars. The buccinator groove is quite shallow. In contrast to the horizontal ramus, the posterior main muscle-bearing structures are surprisingly robust. In particular both the masseteric canal and pterygoid fossa are very large and swollen. The mandibular foramen in the pterygoid fossa is also of large size. Although broken off at its base, enough of the ascending ramus survives to indicate the presence of a steeply inclined coronoid process.

I/1. The I/1, although known only from its posterior portion on the referred specimen, was clearly small and slender relative to that of *Protemnodon tumbuna*. It also retains a well-defined ventral enamel flange that extends posteriorly to the base of the crown. The tooth is heavily worn but the remnants of a distinct dorsal enamel flange can be seen.

P/3. The P/3 of the holotype of *Protemnodon nombe* is almost complete and only slightly worn. Only a sliver of enamel from the anterior-most portion of the tooth is missing. The occlusal edge is straight and of even height. The anterior cuspid forms a distinct prominence and is flanked by a sharp ridge lingually and a blunter one buccally. On the referred specimen a sharp ridge can be seen to descend anteriorly also. Three ill-defined buccal and lingual ridgelets are present on the crest posterior to the anterior cuspid. The posterior cuspid is ill-defined and is the broadest part of the tooth. It is slightly swollen buccally. A slight crest runs down the posterolingual portion of the tooth.

Lower molars. The M/2 of the holotype is heavily worn and enamel is broken away

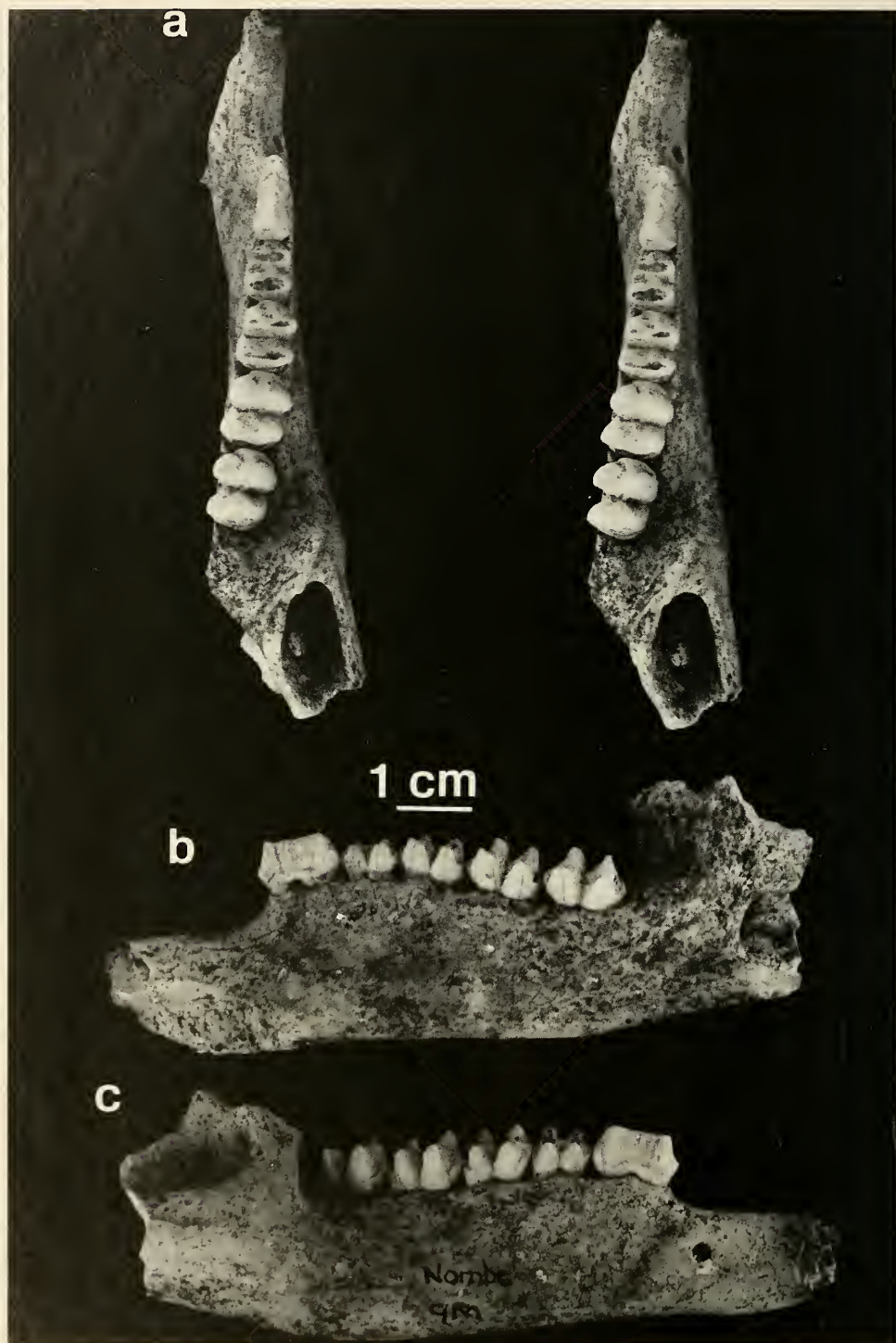


Fig. 6. a, buccal view, b, lingual view and c, stereopair of occlusal view of holotype of *Protemnodon nombe* (PNG/82/40/23), right dentary containing P/3, M/2-5.



Fig. 7. a, buccal view and b, stereopair of occlusal view of referred specimen of *Protemnodon nombe* (PNG/82/40/19), left dentary containing I/1, P/3, M/2-5.

from the metaconid. An ill-defined straight paracristid and cristid obliqua can be discerned. A well-defined posterior cingulum is the best-preserved structure on the tooth. Buccally it reaches the tooth margin, but lingually it terminates about 1.5 mm buccal of it.

The M/3 of the holotype is in a more moderate stage of wear. However, the enamel of both lophids is breached. M/3 is larger than M/2 and the protolophid and hypolophid are subequal in width. It is much broader in the holotype than in the referred specimen. The anterior cingulum is low and anteroposteriorly short. Lingually it runs to near the tooth margin while buccally it terminates about 2 mm from the tooth edge. The paracristid is low, running from just buccal of the tooth midline (its exact relationships are obscured by wear) to the anterior cingulum. Its relationship to the protoconid is obscured by wear. The cristid obliqua is low and worn. It originates just buccal of the tooth midline but its exact relationships are obscured by wear also. A well-developed posterior cingulum is present on the rear face of the hypolophid. It terminates before reaching the buccal edge of the tooth.

M/4 differs from M/3 in the holotype in the following ways. It is larger and less worn. The lingual margins of the lophids are distinctly bowed while the buccal margins are vertical. A distinct fissure frustrates contact of the lingual end of the protolophid with the anterior cingulum (this detail is obscured by wear on M/3). A well-developed premetacristid runs directly anterior from the lingual margin of the protolophid. The M/4 of the holotype is broader than that of the referred specimen.

The M/5 of the holotype is virtually unworn. It differs from M/4 in the following ways. The protolophid is broader than the hypolophid. The protolophid is of an unusual morphology. Buccal to the paracristid the protolophid apex runs along the midline of the loph. Lingual to the paracristid, however, it is shifted posteriorly, giving the anterior face of the protolophid a convex surface in this region. This may have been the case on M/4 also, but this region is obscured by wear. A strong premetacristid runs anteriorly from the lingual end of the protolophid at a 90 degree angle. A preentocristid runs anteriorly from the entoconid, then swings sharply buccally to end against the posterior surface of the protolophid 2 mm from the lingual margin of the tooth. The posterior cingulum is more weakly developed than on M/4. The M/5 of the holotype is broader than that of the referred specimen, and the posterior cingulum is more strongly developed.

Discussion: *Protemnodon nombe* is the rarest macropodid in the fauna of the Nombe rock shelter, being known from two specimens representing two individuals. The species is interesting in that it displays an unusual combination of very primitive dental characteristics and a specialized mandibular morphology. Among the species of *Protemnodon*, the combination of very low-crowned and weakly ridged molars, only moderately elongate premolar and non-specialized lower incisor probably represent the basic dental groundplan. Within the limits of our present knowledge of its dental morphology, *P. nombe* could be considered the most primitive member of the genus. The dentary of *P. nombe*, however is highly unusual and probably derived in morphology. It is large relative to molar size and thus the species could be described as being microdont in the sense that Wells and Murray (1979) describe *Simosthenurus maddocki*. Also striking are the greatly enlarged muscular fossae of the posterior ramus. The functional implications of this peculiar morphological complex are not immediately apparent, and clearly warrant further investigation. However, such features are seen among the species of *Simosthenurus*, a group which, as far as is known, failed to reach New Guinea, and for which *P. nombe* may be an ecological vicar. As with *P. tumbuna*, the low-crowned molars of *P. nombe* suggest a browsing diet and probable rainforest habitat.

DISCUSSION

The macropodids of the Nombe rock shelter shed light on several areas of kangaroo zoogeography and evolution. The New Guinean mammal fauna appears to be a relict one, similar assemblages, at least at the generic level, being found in late Tertiary fossil deposits in Australia (e.g. Turnbull and Lundelius, 1970). The extinct Pleistocene *Protemnodon* species from Nombe support this hypothesis, as they are closest in morphology to Pliocene New Guinean and (more distantly) to Pliocene Australian forms.

Filters obviously existed between New Guinean and Australian montane rainforest areas, as many forms, including potoroids, present in montane rainforests in Australia are not known from New Guinea. Indeed, the New Guinean macropodid assemblage is remarkably limited at higher taxonomic levels, all living and extinct forms belonging to the subfamily Macropodinae. A much richer source of material from which the New Guinean assemblage was derived existed in late Tertiary Australia, where four subfamilies are known. Apart from *Prionotemnus agilis* and *Thylogale stigmatica*, which are found in lowland southern New Guinea, and are probably recent immigrants from Australia, the macropodid fauna of New Guinea is endemic. The living and extinct endemic New Guinean macropodids consist of the species of five genera (*Thylogale*, *Dorcopsulus*, *Dorcopsis*, *Dendrolagus* and *Protemnodon*). The last two have undergone minor radiations within New Guinea. The species of *Dorcopsis* and *Dorcopsulus* together are probably monophyletic, and thus the entire montane macropodid fauna of New Guinea can be accounted for by the initial presence of only four original kinds of kangaroos. All are similar in that they represent primitive kinds of macropodines.

The fossils of the Nombe rock shelter allow a comparison of late Pleistocene extinction in New Guinea and Australia. Of the mammals from Nombe, the four largest species of herbivore are extinct. These include a species of pig-sized diprotodontid, two species of *Protemnodon* (grey kangaroo sized and smaller) and a tree kangaroo slightly larger than *Dendrolagus dorianus*. Of these species, at least the macropodids are inferred on the basis of dental morphology to have lived in rainforest, and not 'shrub-rich treefern grassland', as has been previously postulated (Hope and Hope, 1976). Interestingly, there is no evidence for post Pleistocene dwarfing in New Guinean macropodids, a phenomenon so prevalent in larger Australian macropodid lineages (Marshall and Corruccini, 1978). There is also no evidence of size overlap between living forms and those which became extinct in the late Pleistocene, the converse of which is true in Australia. In New Guinea, the cut off size between living and extinct forms is sharp. Those with an adult bodyweight of over 18 kg became extinct, whilst smaller forms survived. The very association of man and megafauna at Nombe is unusual in the Australian context at present, and may denote a real difference in the causes of extinction in the two areas. Finally, there is some evidence that some megafaunal species at Nombe survived to 14,000 years BP or later. In Australia, although megafaunal elements may have survived until as recently as 16,000 BP (Hope *et al.*, 1977), most sites containing megafaunal elements are older, (e.g. Lancefield, about 25,000 BP, Gillespie *et al.*, 1978).

The terminal Pleistocene period was one of quite dramatic climatic change in the New Guinea highlands. Glaciation was probably extensive throughout the period of deposition of the red-brown clay (stratum D), and the treeline may have been depressed to just above the altitude of the Nombe rock shelter. On nearby Mt Wilhelm deglaciation was underway by 14,000 years BP and virtually complete by 10,000 years BP. However, it may have taken a further 5,000 years before vegetation stabilized into modern communities (Hope and Hope, 1976). The terminal Pleistocene also saw

initial agricultural experiments at mid-montane altitudes, possibly causing further vegetational disruption at this time. However, the effect of both human disturbance and changing climate on vegetational parameters is as yet poorly known, and it would be premature to attempt to assess the impact of such factors on the mammalian fauna.

CONCLUSIONS

1, The three larger species of macropodid from Nombe rock shelter are newly-described extinct forms (*Dendrolagus noibano*, *Protemnodon tumbuna* and *P. nombe*); the four smaller species represented in the site are extant and previously known.

2, *Protemnodon tumbuna* and *P. nombe* are both primitive species of *Protemnodon*, but they display some unique specializations.

3, Megafaunal species in New Guinea appear not to have undergone post-Pleistocene dwarfing and may have persisted longer than their counterparts in Australia.

4, While man and megafauna apparently co-existed for an extended time in the Nombe area, the extent and nature of their interaction is still unclear.

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